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Nitrogen Saturation in Northern Forest Ecosystems
Excess Nitrogen from Fossil Fuel Combustion
May Stress the Biosphere

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16. ABSTRACT

In this article we provide a formal definition of nitrogen saturation and set forth a series of testable hypotheses regarding the states of forest ecosystem response to chronic nitrogen deposition. These hypotheses are used to suggest early indicators of nitrogen saturation and to discuss the potential implications of nitrogen saturation of forest ecosystems over large geographic areas. Possible effects include elevated concentrations of nitrate, aluminum, and hydrogen in streams, which would decrease water quality; frost damage or other disruptions of physiological function that would reduce productivity in confifer stands; increase cation leaching from soils and nitrate losses that would lead to reduced soil fertility and increased acidity; and possible increases in emissions of trace gases such as nitrous oxide, which may alter atmospheric chemistry and contribute to the warming of Earth's atmosphere (the greenhouse effect).

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Nitrogen Saturation in Northern Forest Ecosystems

Excess nitrogen from fossil fuel combustion may stress the biosphere

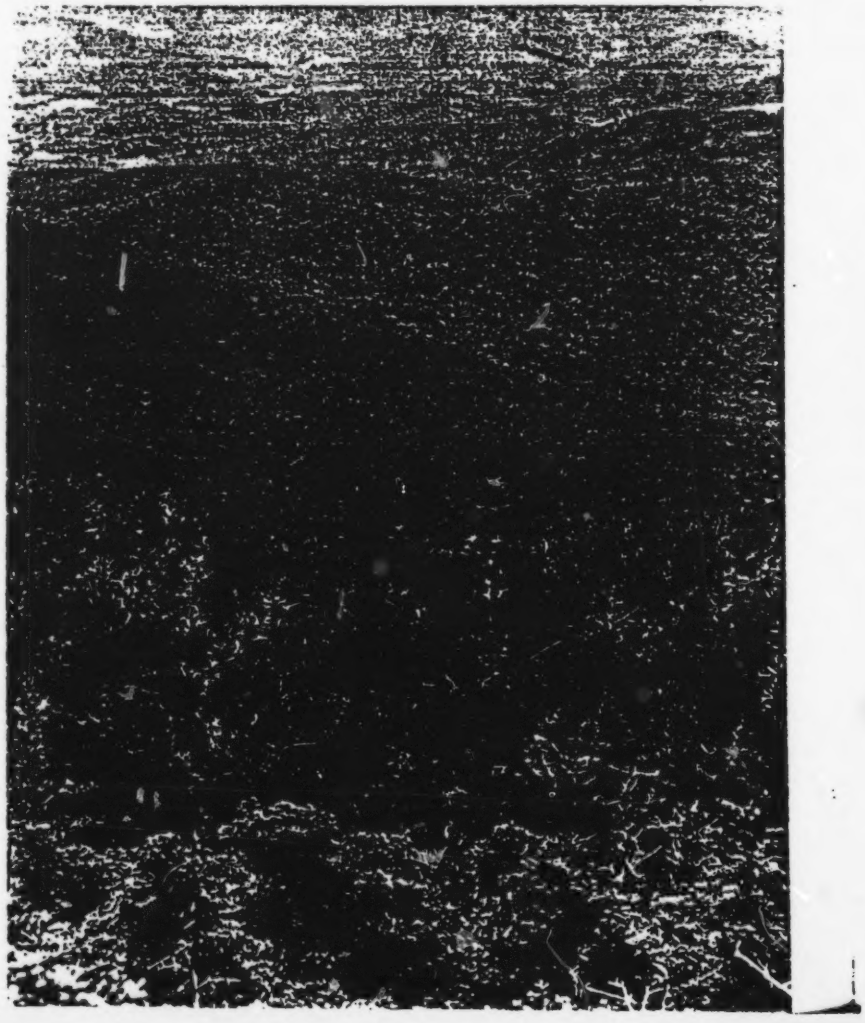
John D. Aber, Knute J. Nadelhoffer, Paul Steudler, and Jerry M. Melillo

Human activity has greatly altered the biogeochemical cycles of Earth, generally increasing pollutant concentrations in the atmosphere and deposition rates to the surface. The combustion of fossil fuels is a major component of human impact on the atmosphere and biosphere. Acid deposition, or acid rain, is one important phenomenon associated with the burning of coal, gasoline, and oil. Until recently, sulfur emissions and sulfuric acid deposition have been the focus of US regulation on acid rain. There is, however, increasing concern about the nitrogen component of emissions and its potential effects on air quality, water quality, and the health of forest ecosystems.

Nitrogen emissions can have direct effects on air quality, through both the oxidizing potential of nitrogen oxides and the role these compounds play in the formation of ozone. The effects on water quality and on forest nutrition and health are more complex.

Most forest ecosystems in the humid temperate regions of the world that are now experiencing increased nitrogen deposition have been traditionally considered nitrogen limited. Fertilizer experiments generally show tree growth responses only to the nitrogen component. Most northern forests are efficient at retaining added nitrogen, from either precipitation or

View from the top of Camels Hump in northern Vermont. Upper slopes were formerly dominated by red spruce trees, whose dead trunks can be seen in the foreground rising from the reforming forest canopy. This site has been used as part of an extensive survey of effects of long-term nitrogen additions on forest ecosystem function, including nitrous oxide and methane fluxes from soils.



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fertilizers, and only certain forest types show significant losses of nitrate to streams, even after major disturbances (Vitousek et al. 1979). The general agreement that unaffected forests are usually nitrogen limited has perhaps delayed acceptance of the idea that increased nitrogen deposition is a potential source of stress.

Rates of nitrogen addition to forest ecosystems through wet and dry atmospheric deposition material range from less than 2 kg $N \cdot ha^{-1} \cdot yr^{-1}$, in areas largely unaffected by industrial sources, to more than 40 kg $N \cdot ha^{-1} \cdot yr^{-1}$ at high elevations in New England (Lovett et al. 1982, Parker 1983). Recent evidence of direct uptake of gaseous HNO_3 by foliage may increase these numbers somewhat (Norby in press).

Even these higher values are quite low relative to experimental or commercial rates of fertilizer addition (generally in the range of 100 to 400 kg $N \cdot ha^{-1}$). However, there is a fundamental difference between these sources of nitrogen. Fertilizations are generally one-time applications, whereas atmospheric deposition is chronic. Pulse fertilizer additions may lead to short-term increases in nitrogen cycling and forest productivity, but these effects disappear after several years, as the added nitrogen is sequestered in wood and soil organic matter.

By contrast, elevated nitrogen deposition represents a continuous addition to background nitrogen availability due to mineralization of organic matter (20–75 kg $N \cdot ha^{-1} \cdot yr^{-1}$ in coniferous stands and 50 to 150 kg $N \cdot ha^{-1} \cdot yr^{-1}$ in deciduous stands; Gosz 1981, Melillo 1981, Nadelhoffer et al. 1985, Pastor et al. 1984). Over time, these additions may exceed the capacity for nitrogen uptake and retention by plants, soils, and microbes.

In the past five years, evidence has accumulated suggesting nitrogen availability in certain forest ecosystems in excess of plant and microbial demand. Nihlgard (1985) described, adjacent to agricultural areas, woodlands where ammonium deposition greatly exceeded biological uptake potential. Friedland et al. (1984) identified winter frost damage to foliage as a factor contributing to spruce decline in New England, and they suggested excess nitrogen content in foliage is a hindrance to the development of frost-hardiness. Recent reports of increased losses of nitrate from forest soils during spring snowmelt, and during the growing season, have been associated with increased deposition of nitrogen and perhaps with reduced plant demand (Johnson et al. in press, Rascher et al. 1987).

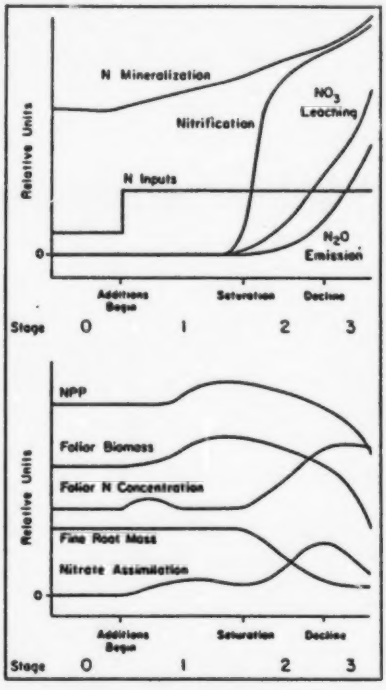

Figure 1. Hypothesized time course of forest ecosystem response to chronic nitrogen additions. Top: changes in nitrogen cycling and nitrogen-loss rates. Bottom: plant responses to changing levels of nitrogen availability. The four stages (0–3) correspond to those described by Smith (1974) and Bormann (1982) for ecosystem response to pollution loading. Stage 0 is the pre-treatment condition. In stage 1, increased deposition is occurring, but effects on the ecosystem are not evident. For a limiting nutrient such as nitrogen, a fertilization effect might result in increased ecosystem production and tree vigor. In this stage, retention of nitrogen is most efficient, and that retention does not damage, and may enhance, ecosystem function. In stage 2, negative effects occur, but they are subtle, nonvisual, and/or difficult to measure. Only in stage 3 do visible effects occur, resulting in major environmental impacts. Different species and environmental conditions could alter the timing of effects. This scenario is for a species such as red spruce, in which nitrate reductase activity in foliage is low or absent.

These results and others have given rise to the variously defined concept of *nitrogen saturation* (Skeffington and Wilson 1988). In this article we provide a formal definition of this concept and set forth a series of testable hypotheses regarding the stages of forest ecosystem response to chronic nitrogen deposition. These hypotheses are used to suggest early indicators of nitrogen saturation and to discuss the potential implications of nitrogen saturation of forest ecosystems over large geographic areas. Possible effects include elevated concentrations of nitrate, aluminum, and hydrogen in streams, which would decrease water quality; frost damage or other disruptions of physiological function that would reduce productivity in conifer stands; increased cation leaching from soils and nitrate losses that would lead to reduced soil fertility and increased acidity; and possible increases in emissions of trace gases such as nitrous oxide, which may alter atmospheric chemistry and contribute to the warming of Earth's atmosphere (the greenhouse effect).

Definition of nitrogen saturation

Nitrogen saturation may be defined as the availability of ammonium and nitrate in excess of total combined plant and microbial nutritional demand. (This definition excludes the use of nitrate as a substrate for denitrification.) By this definition, nitrogen saturation can be determined simply by the accumulation of mineral nitrogen in soils (generally as ammonium in humid areas) or by increased leaching of nitrate or ammonium below the rooting zone. Increases should be considered in comparison with background levels occurring in unaffected forests, because all systems show low levels of ammonium accumulation and/or nitrate leaching. Saturation implies limitations on biotic function by some other resource (e.g., phosphorus or water for plants or carbon for microbes). This definition combines attributes of several approaches current in the European literature (Skeffington and Wilson 1988).

Stages in the development of nitrogen saturation

Forest ecosystem response to chronic, elevated nitrogen additions involves a complex interaction among the major processes affecting nitrogen cycling. These include deposition, plant uptake and allocation, litter production, immobilization and mineralization during litter and soil organic matter decay, nitrification, ion leaching, and trace gas emissions. Figure 1 presents an integrated set of hypotheses on the time course of change in major nitrogen cycling processes in response to nitrogen deposition.

In Figure 1, ecosystem responses are separated into the four stages of pollution deposition impact on ecosystems developed by Smith (1974) and Bormann (1982). Here, the nitrogen source could be either pollution or experimental application. For simplicity, nitrogen inputs in Figure 1 are described as a step increase, representing a chronic, continuous experimental addition designed to emulate atmospheric deposition.

Stage 0—Characteristics of nitrogen cycling under nitrogen-limiting conditions. At background levels of nitrogen deposition, northern temperate forest ecosystems generally experience suboptimal nitrogen availability and show significant increases in tree growth in response to nitrogen additions (Lea et al. 1980, Mitchell and Chandler 1939). Net primary production is controlled by the amount of nitrogen made available on an annual basis through net mineralization from organic matter (plus low levels of nitrogen deposition) and the nitrogen-use efficiency of the vegetation (Vitousek 1984). Foliar biomass expresses the productive potential of the site, and nitrogen concentration in foliage is within the narrow range of values typical for the species present (Aber et al. in press).

In systems with suboptimal nitrogen availability, litter decomposition is also nitrogen limited in that additions of nitrogen will both speed the decay process and increase the amount of nitrogen immobilized during the early stages of that process (Melillo et al. 1984). This acceleration is due in part to effective retranslocation of nitrogen from senescing foliage, which creates nitrogen-poor litter material (Flanagan and Van Cleve 1983). Poor litter quality and low soil pH combine to restrict soil macrofauna activity, resulting in the accumulation of a substantial forest floor (O horizon).

We have found that both the presence of an O horizon and low soil pH are associated with the absence of nitrification. Nitrification is the microbial conversion of ammonium, generated by the decomposition of soil organic matter, to nitrate. It is a critical process in forest ecosystems because nitrate and ammonium behave differently in soils.

In a study of more than 30 forest soils in Wisconsin and Massachusetts, we found that all soils in which more than 50% of the mineralized ammonium was nitrified had mull forest floors (well-mixed with mineral soil), whereas all those with less than 50% nitrification had moder or mor (poorly mixed) forest floors. With few exceptions, nitrification was absent in soil horizons with pH less than 4.2 (measured in 0.01 M $CaCl_2$). In general, both low pH and limited ammonium availability are thought to reduce nitrification in forest ecosystems (Robertson 1982). In the absence of nitrification, nitrogen uptake and assimilation occur mainly from ammonium pools, although low levels of nitrate assimilation may occur due to wet or dry atmospheric deposition of nitrate.

Stage 1—Initial effects of chronic nitrogen deposition. The standard effects of high-dosage, pulse fertilizations on temperate forest ecosystems are well known. The first response is an increase in foliar nitrogen content. However, elevated nitrogen content is not easily maintained, even under conditions of continuous nitrogen additions (Weetman and Fournier 1984). Higher foliar nitrogen content is generally followed by increases in foliar biomass and a return to background foliar nitrogen levels (Binkley and Reid 1984, Safford and Filip 1974). Higher foliar biomass results in increased tree growth, which may persist for several years. In some cases, a permanent improvement of site quality and tree growth occurs (Binkley and Reid 1985). However, even several years of heavy nitrogen addition may result in no discernible increase in nitrogen mineralization from the large, slowly decaying soil humus pool (Miller et al. 1976).

Fertilization generally decreases mycorrhizal infection of roots (Marx et al. 1977) through lower allocation of carbon by plants to root symbionts, but effects on root turnover are still subject to debate (Aber et al. 1985, Lauenroth et al. 1986, Vogt et al. 1986). Reduced retranslocation of nitrogen from senescing foliage is another common response to fertilization (Flanagan and Van Cleve 1983), leading to higher nitrogen content in litter and faster decay rates. Only with additions of urea, from which the mineralization of ammonium causes a temporary increase in soil pH, has fertilization been linked with the induction of nitrification in soils.

The results of pulse fertilization studies may be of limited value in inferring the effects of chronic nitrogen deposition on forest ecosystems. Although responses to pulse additions may be more striking, chronic additions are likely to produce longer-lasting adjustments in system structure and function.

We hypothesize that the lower but constant rates of nitrogen addition due to chronic deposition will not lead to a detectable transient increase in foliar nitrogen concentration, but rather to a gradual increase in foliar biomass with a constant nitrogen concentration. Increases in productivity would likewise be gradual and would likely be unnoticed in the year-to-year variation in tree growth resulting from such factors as climate and herbivory. However, recent summary data from southern Germany suggests some long-term improvement in growth in many stands, perhaps attributable to chronic nitrogen deposition (Kenk and Fischer 1988).

According to this hypothesis, forests that are repeatedly harvested or burned, and so experience a continual removal of nitrogen, would continue to assimilate nitrogen inputs, and they would probably be healthier and more productive because of those inputs. Unmanaged forests would continue to show slow increases in the total nitrogen content of vegetation and soils. There would be little change in the form of nitrogen taken up, in fine-root biomass, and in gaseous or dissolved losses.

Figure 2. Aerial photo of Harvard Forest in Petersham, Massachusetts, showing the main office, laboratory, greenhouse, and residential buildings, plus the mixture of hardwood and coniferous forests used for long-term research. Photo: courtesy Harvard Forest Archive.

Stage 2—Nitrogen saturation. Upland forest ecosystems have a finite capacity to assimilate and retain nitrogen. With the exception of cation exchange retention of ammonium, there are no important abiotic soil reactions that retain mineral nitrogen in the soil. Nitrogen retention in these systems occurs largely through biotic uptake of mineral nitrogen or through the incorporation of nitrogen into decaying soil organic matter. As mineral nitrogen in soil increases, biotic uptake, either plant or microbial, becomes limited by the availability of the other resources essential for growth.

Nitrogen saturation is reached when availability, through both current atmospheric deposition and mineralization of previously accumulated soil nitrogen, exceeds the biotic uptake capacity of the system. Stated another way, it occurs when other essential resources limit plant and microbial growth. In temperate systems, the primary candidates for this secondary limiting factor include water and phosphorus. On exceptionally rich and well-watered sites, a full canopy may cause light to become limiting.

We hypothesize that nitrogen saturation will result in at least one of the following: permanently elevated nitrogen concentration in foliage (e.g., Lang et al. 1982) and perhaps elevated amino acid content (Margolis and Waring 1986); lowered phosphorus and lignin content in foliage (e.g., Waring et al. 1985); and increased water stress. Each of these results reflects relatively lower availability of carbon, phosphorus, or water within the plant as nitrogen limitations are removed. Recent successes in the measurement of lignin content of whole forest canopies by remote sensing (Wessman et al. 1988) suggest it is possible to use these foliar chemistry responses to detect the earliest stages of nitrogen saturation and to map its occurrence over large areas.

By itself, nitrogen saturation need not have a negative impact on forest ecosystem health or function. Brief periods of nitrogen saturation after commercial fertilization have generally positive effects on productivity in the short term, often leading to greater biomass accumulation in the long term. Long-term occupation of temperate forest soils by tree species supporting symbiotic nitrogen fixation may result in naturally occurring high nitrogen mineralization rates, high nitrification rates, and some nitrogen leaching losses (Vitousek et al. 1979), as well as increased forest productivity (Binkley et al. 1984).

Increased nitrogen availability relative to plant demand may result in slightly lower fine-root and mycorrhizal biomass. However, as long as ammonium remains the dominant form of nitrogen made available, fine-root mass will remain high.

One potentially negative effect is the reported loss of frost-hardiness in certain conifer trees receiving high doses of nitrogen fertilization (Soikkeli and Karenlampi 1984). Loss of needles and greatly reduced productivity have been reported. The possibility of nitrogen saturation leading to frost damage and eventual tree decline has been raised for spruce-fir forests in the northeastern United States (Friedland et al. 1984). Heavy, continuous fertilization has also led to accelerated tree death, in excess of that resulting from faster tree growth and self-thinning, in jack pine in Quebec (Weetman and Fournier 1984).

Nitrification is a pivotal process. As nitrogen deposition to the saturated ecosystem continues, we expect ammonium levels in the soil to increase. We hypothesize that accumulation of excess ammonium in soils will induce nitrification, even at low soil pH. Novick et al. (1984) measured significant rates of nitrification in Adirondack mountain soils at pH values as low as 3.5. An extensive survey of nitrification potentials in high-elevation spruce-fir forest floors in Maine, New Hampshire, Vermont, and New York showed that nitrification increases from east to west linearly with regional trends of increasing nitrogen deposition.[1] High rates of nitrification have been reported in disturbed forest ecosystems, where nitrogen availability greatly exceeds plant de-

[1]S. G. McNulty and J. D. Aber, 1989, unpublished data.

mand, even at low soil pH (Smith et al. 1968).

Induction of nitrification can lead to several changes in ecosystem structure and function. These include:

- Nitrate leaching from soils. Soil acidification effects of acidic deposition are tightly coupled with increased anion movement through soils and the accompanying loss of nutrient cations (Reuss and Johnson 1986). Currently, sulfate is the major anion of pollutant origin driving soil acidification in those soils where sulfate sorption potential is either low or has been overwhelmed by high sulfate concentrations. Nitrification in a nitrogen-saturated stand will result in a nitrate breakthrough—elevated nitrate concentration and loss in soil leachate. The effect of this nitrification on total anion leaching loss from forests could be considerable. Elevated losses of aluminum in conjunction with high nitrate leaching have been reported for spruce stands in the Great Smoky Mountains (Johnson et al. in press) and during peak spring runoff into small lakes in the northeastern United States (Driscoll et al. 1987).
- Increased emissions of nitrous oxide, an important greenhouse-effect gas. N_2O can be released either during the nitrification process (Bremner and Blackmer 1978) or as a result of denitrification (Firestone et al. 1980). How ecosystem nitrogen losses would be partitioned between nitrate and nitrous oxide is a critical question with important policy implications. Nitrate degrades water quality, whereas nitrous oxide emissions affect atmospheric chemistry and contributes to climate change.
- Fine-root dynamics and forest floor structure. Based on our previous studies of fine roots (Aber et al. 1985, Nadelhoffer et al. 1985), we hypothesize a large reduction in biomass and perhaps a loss of ectomycorrhizal symbionts after the onset of nitrification. This phenomenon is linked to the greater mobility of nitrate in soils relative to ammonium and the ability of fine roots to more fully occupy the soil when nitrogen is available in the nitrate form. We further hypothesize that this change in rooting density will result in at least a partial reduction of forest floor mass and increased mixing of organic matter into the mineral soil.

The summary effects of nitrogen saturation, and these ecosystem responses to it, would include a measurable increase in nitrate leaching, approaching nitrogen deposition input levels; measurable increases in the efflux of nitrous oxide to the atmosphere; and measurable, but subtle changes in ecosystem structure and chemistry. The most important change, to which these all contribute, is that the ecosystem would no longer function as a nitrogen sink. Rather, it would be converting nitrogen in atmospheric deposition to groundwater nitrate, which reduces water quality, and to nitrous oxide, a greenhouse-effect gas. These effects could occur without the dramatically visible changes associated with forest decline.

The cumulative nitrogen deposition load required to saturate forest ecosystems, to bring them into stage 2, is a critical unknown. Undoubtedly the initial rate of nitrogen mineralization, the uptake potential of the vegetation, the availability of other resources such as water and phosphorus, and the nitrogen deposition rate will all enter into the calculation. Perhaps the most critical unknown is the degree to which excess nitrogen can be sequestered into soil humus. Small changes in the carbon-nitrogen ratio of soil organic matter could result in large changes in nitrogen storage. In general, there is almost no information on the rate at which nitrogen mineralization will increase in response to increased nitrogen input. We are attempting to answer such questions through a series of experimental nitrogen additions to different forest types.

Stage 3—Forest decline. Hypotheses presented for stages 1 and 2 involve only minor extensions of existing knowledge about temperate forest ecosystem function. Hypotheses that predict stage 3, the visible disruption of forest structure through tree death (forest decline), are more tenuous. Still, there are several ways by which excess nitrogen availability could lead to reductions in plant productivity and even to mortality.

As one example, excess ammonium availability has been linked to nutritional imbalances and yellowing of foliage in heavily affected areas in the Netherlands (Van Dijk and Roelofs 1988). This report may be the first of toxic levels of nitrogen under field conditions.

Alternatively, reduced fine-root biomass could have important implications for the availability of other resources to plants, particularly water and phosphorus. Both reduced root

Figure 3. Backpack application of nitrogen additions to research plots in the red pine stand at Harvard Forest.

mass and mycorrhizal infection are basic characteristics of declining conifer forests in both Europe and the United States. Low phosphorus content has been noted in foliage of conifers in high-deposition areas of the United States (Lang et al. 1982). Drought has been implicated in either triggering or exaggerating forest decline (Foster and Reiners 1983, Johnson and Siccama 1983).

For certain species, nitrate uptake could pose an additional stress. Nitrate must be reduced to ammonium before it can be incorporated into amino acids. It was long argued that forests maintained an ammonium economy through the allelopathic inhibition of nitrification (Rice and Pancholy 1972), partly in response to the selective pressure to avoid the energy costs of nitrate reduction. However, nitrate reduction can occur either in foliage or in roots. If it occurs in roots, it is driven by respiration and can represent a drain on the carbohydrate pool in the plant. If it occurs in foliage, it can be driven by excess reductant from the light reactions of photosynthesis and thus have little or no effect on total photosynthate pools.

We have compared productivity in several forests with similar species composition and total nitrogen availability but that differ in the form of nitrogen that is taken up (nitrate versus ammonium). Results show no effect on net primary production (Aber et al. 1983, Nadelhoffer et al. 1985, Pastor et al. 1984). We have also measured significant foliar nitrate reductase activity in foliage of several of these stands, and we observed increasing foliar nitrate reductase rates along a gradient of increasing nitrate uptake.[2]

These results are in agreement with recent studies that show substrate induction of nitrate reductase activity in foliage for the majority of woody species (Smirnoff et al. 1984). However, maximal inducible nitrate reductase levels vary among species, with conifers showing generally less response than angiosperms. Also, this pathway requires that reductant from the light reactions of photosynthesis be available.

Consider the example of red spruce (*Picea rubens*). Although the induction of nitrate reductase activity has been shown in the foliage of this species in response to nitric acid gas exposure (Norby in press), there is at least one report of no foliar reductase activity in response to nitrate in nutrient solution (Yandow and Klein 1986). In New England and throughout the Appalachians, red spruce tends to grow at high elevations, particularly where cloud cover is frequent (Siccama 1974). If either the genetic capacity for foliar production of nitrate reductase is low, or cloud cover results in low levels of available reductant in foliage, then nitrate reduction in either root or foliage will represent a net drain on the carbohydrate pools in the plant. If nitrate reductase activity is too low, then nitrate can accumulate to levels in foliage that are potentially toxic, particularly for conifers (Waring 1988).

Although plant adaptations to these contingencies could result from natural selection, it is conceivable that excess nitrogen availability is such a novel form of stress in certain forest types that such selection has not occurred (Waring 1988). In certain species, nitrogen availability may be the environmental signal that determines carbon allocation to roots. Reductions in fine-root biomass may exaggerate any nitrogen-phosphorous imbalances in leaves, or they may increase water stress. On the other hand, normally adaptive changes in root-shoot allocation patterns may be made nonadaptive by the interactions of nitrogen saturation with other forms of air pollution.

Stage 3 begins when one or all of the above mechanisms reduces total net photosynthesis and begins to reduce productivity (Figure 1). This reduction would further exacerbate the lack of photosynthate for root production, and it would initiate a positive feedback resulting in further declines in tree growth and eventually in tree death.

Whether or not nitrogen saturation is playing a role in today's forest decline remains to be shown. However, initiation of forest decline in nitrogen-saturated stands, by whatever mechanism, could have important implications for water quality and atmospheric chemistry. Removal of the forest canopy will increase decomposition of organic matter and mineralization of nitrogen. Nitrogen accumulated in both vegetation and soils during stage 1 will begin to be released. At this point, nitrogen losses from the system would be higher than inputs, perhaps substantially so (Bormann and Likens 1979). The partitioning of these losses between nitrate in solution and N_2O to the atmosphere would be crucial in determining their overall environmental effects.

Interactions with other forms of air pollution

Nitrogen deposition is only one form of air pollution to which forests in industrial regions are exposed. There may be significant interactions with other forms of pollution that enhance or suppress the nitrogen effects.

Ozone and other oxidants are receiving increasing attention as important stresses on forest ecosystems and possible contributors to forest decline. The major effect of ozone on forests is the reduction of net photosynthesis as a linear function of total dose (hours × concentration; Reich and Amundson 1985). As nitrogen saturation is, in effect, excess nitrogen for the given amount of photosynthate produced by the plant, ozone exposure could speed the occurrence of nitrogen saturation and magnify its effects. Nitrogen deposition and ozone could act synergistically in inducing nitrogen saturation and perhaps forest decline.

Nitrogen deposition may also have synergistic effects with sulfate. Once nitrogen saturation occurs and nitrate losses begin, nitrate will add to the anion leaching–soil acidification potential attributable to sulfate. In soils with significant sulfate sorption potential, a nitrate breakthrough could initiate significant anion leaching in soils previously protected from this form of soil acidification.

In contrast, heavy-metal pollution may to some extent suppress the effects, or delay the occurrence, of nitrogen saturation. Heavy metals accumulate primarily in the forest floor where they act to reduce decomposition and net mineralization through the suppression of enzyme activity (Ebregt and Boldewijin

[2]K. J. Nadelhoffer, 1989, unpublished results.

Figure 4. Structure of red spruce stands on Mt. Ascutney, Vermont, used for experiments on the effects of chronic nitrogen additions on forest growth, nitrification, and nitrate mobility in soils.

1977). To the extent that decomposition is reduced, the potential for accumulating nitrogen in organic form is increased and nitrogen saturation is postponed. However, Friedland et al. (1986) have suggested that heavy-metal concentrations in forest floors of the northeastern United States are not currently high enough to affect decomposition significantly.

Ongoing research on nitrogen saturation

The hypotheses outlined here are currently being tested by chronic nitrogen-addition experiments in four different forest types. Long-term additions of both ammonium nitrate (two dose levels) and ammonium nitrate plus sulfate are a major activity at the Harvard Forest Long-Term Ecological Research site (Figure 2) in Petersham, Massachusetts. Additions are made monthly during the snow-free season to both red pine and mixed hardwood sites (Figure 3). Nitrous oxide and methane fluxes from soils are being measured along with net primary production and rates of nitrogen cycling and leaching.

Also supported by the National Science Foundation are a series of nitrate, ammonium, and combined ammonium nitrate additions to high-elevation red spruce stands on Mt. Ascutney in Vermont (Figure 4). This study emphasizes fertilization effects on plant production and foliar chemistry and is also monitoring any nitrification induction and the mobility of nitrate in soils.

The Watershed Manipulation Project, supported by the US Environmental Protection Agency (EPA), is conducting both plot-level and watershed-level experiments on the effects of acid deposition on water quality. A series of experimental northern hardwood plots are located near the base of the paired experimental watersheds on Lead Mountain in eastern Maine (Figure 5). These are receiving combinations of nitrate and sulfate additions in the form of weekly spray irrigations. A large team of researchers from several universities is examining the full range of physical, chemical, and biological responses, including processes related to nitrogen saturation.

Finally, an extensive survey of spruce-fir stands throughout New England and New York is nearing completion. More than 160 sample sites have been assayed for nitrogen mineralization and nitrification potential, as well as for associated changes in foliar chemistry. The National Aeronautics and Space Administration has provided partial funding for this work, one of the purposes of which is to test the potential for remote-sensing instruments to detect subtle changes in chemical content of whole forest canopies and to infer changes in ecosystem function over large areas. One aspect of this work was the measurement of nitrous oxide and methane fluxes (Figure 6) from soils on Camels Hump in Vermont, an area experiencing extensive spruce decline.

Conclusions

The ability of temperate forest ecosystems to accumulate nitrogen from atmospheric deposition is limited. Most current assessments of acid deposition on environmental quality assume either unlimited, or at least constant, nitrogen accumulation within forested watersheds. Recent measurements of elevated nitrate leaching from certain high-elevation forests

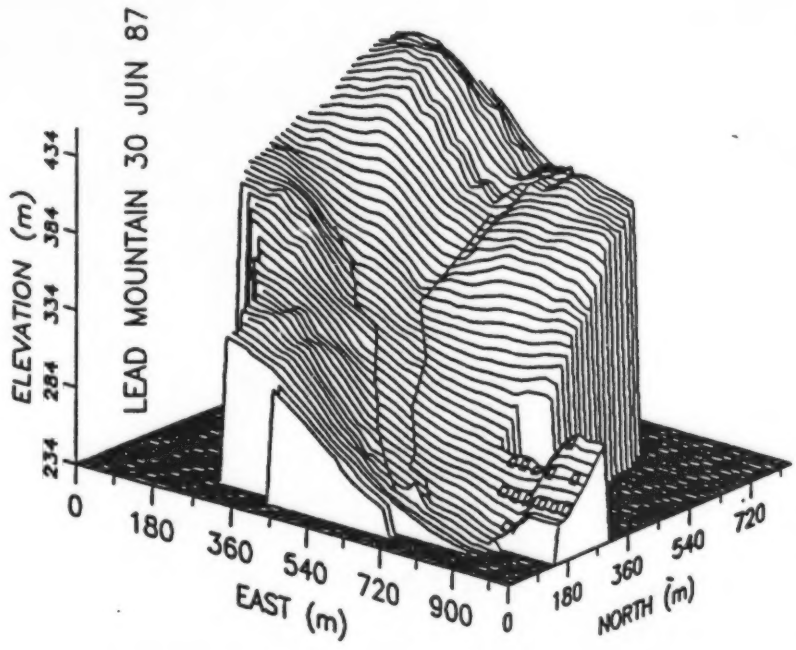

Figure 5. Three-dimensional view of the Bear Brook watersheds on Lead Mountain near Beddington, Maine. Small squares at the base of the watersheds represent the locations of the external experimental plots.

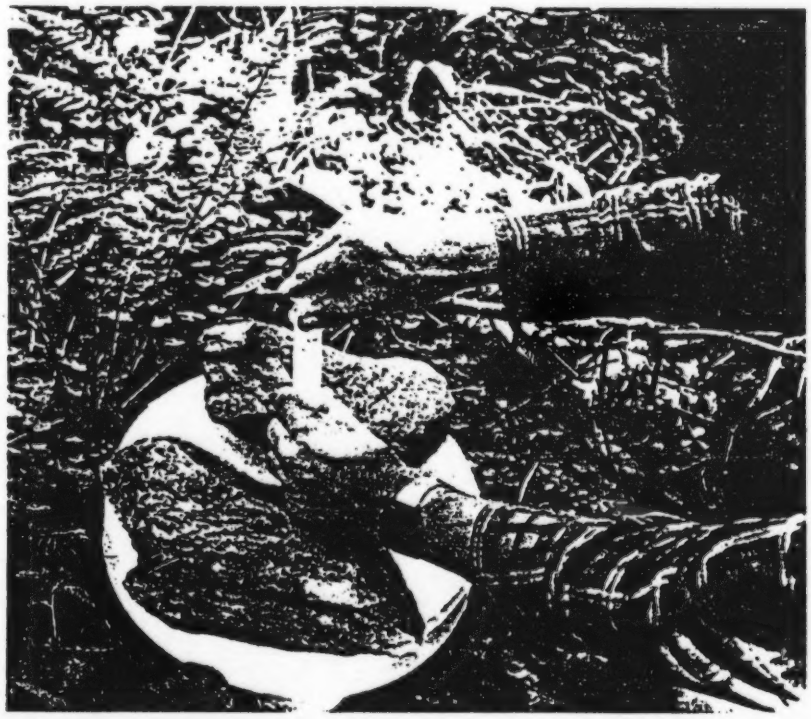

Figure 6. Soil chambers used for measurement of methane and nitrous oxide fluxes from forest soils. Chamber sits on rim pressed firmly onto soil surface, but not penetrating the soil or severing roots. Access port on cover allows extraction of headspace gas samples.

suggest that these forests have reached saturation; cumulative deposition inputs have exceeded the capacity of these systems to accumulate nitrogen.

Excess nitrogen represents a unique form of stress to several types of forest ecosystems in temperate regions. It may lead to reductions in production and perhaps contribute to forest decline. Nitrification and subtle but measurable changes in foliar chemistry may provide an early warning system for nitrogen saturation.

Nitrogen-saturated forests may become net sources of nitrogen, rather than sinks. The environmental effects of nitrogen saturation over large regions could then be considerable in terms of both nitrate leaching to streams and ground water and nitrous oxide flux to the atmosphere. It is time to consider the nitrogen component of acid deposition as at least as serious an environmental threat as sulfate. This perspective should be applied to both the acid-deposition research program and the development of acid-deposition control strategies.

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